Research Article

Community-level trophic characteristics and interactions between native and non-native fish: The example of the Lower Pearl River Basin of China

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Citation: Wei H, Vilizzi L, Zhang M, Jiang Y, Xu M, Fang M, Yu F, Shu L, Wang X, Gu D (2024) Community-level trophic characteristics and interactions between native and non-native fish: The example of the Lower Pearl River Basin of China. NeoBiota 96: 129–149. https://doi.org/10.3897/neobiota.96.129121

Abstract

Aquatic ecosystems can harbour more than one non-native fish species and this can represent a threat due to trophic interactions with native fishes. However, research on interactions amongst multiple co-occurring native and non-native fish remains scarce. In this study, 551 organisms from 44 native fish, 11 non-native fish, 35 macroinvertebrates (of which one was non-native), together with 162 samples of basal resources were collected from six rivers of the Lower Pearl River Basin of China. Nitrogen and carbon stable isotope analysis was used to calculate community-wide trophic metrics and the degree of trophic overlap between native and non-native fish at both the community and functional feeding group level, together with diet composition. At the community level, there was a high degree of trophic niche overlap between native and non-native fish as a result of similarities in trophic characteristics. At the functional feeding group level, both native and non-native functional feeding groups demonstrated the capacity to occupy the niche space of each other. A significant trophic niche overlap, exceeding 50%, was found between non-native detritivorous and omnivorous fish, suggesting competition. The difference in diet composition between some native and non-native fish depended on the category of diet source across the rivers, suggesting dietary segregation. Albeit limited, the present findings suggest that trophic interaction between native and non-native fish is likely to reach a dynamic equilibrium status in the community owing to trophic segregation of fish species and the antagonistic effects amongst non-native fish.

Key words: Diet, impact, multiple invasions, stable isotope analysis, trophic interactions

Introduction

The management and control of non-native species has become a priority for biodiversity conservation, as invasive species are recognised as one of the major drivers of global environmental change (Pyšek et al. 2020). With the accelerating rate of globalisation, a proliferation of non-native species has been documented across an expanding array of countries and regions and this has led to numerous ecosystems facing threats from multiple invasive species (Seebens et al. 2021).

Freshwater ecosystems are particularly vulnerable to invasions by multiple species and especially so by those fishes associated with aquaculture and the aquarium trade (Bernery et al. 2022). However, research has mainly focused on individual non-native fish species, overlooking the intricate interactions amongst multiple co-occurring native and non-native fish (Coughlan et al. 2022). Given that interactions amongst these species can trigger cascading effects throughout the entire food web, gaining a deeper understanding is crucial for devising ecosystem-level management strategies to address multiple species invasions (e.g. Rogosch and Olden (2020)).

The co-existence of species within communities, driven by species interactions, predominantly stems from niche differences (e.g. disparities in environmental requirements), facilitating resource partitioning and reduced interspecific competition (Giam and Olden 2016; Buche et al. 2022). Differences in the niches occupied by native and non-native species can profoundly influence the outcomes of biological invasions (Li et al. 2019). Therefore, a fundamental inquiry regarding the consequences of invasions by multiple non-native fish revolves around whether the trophic niche of co-occurring non-native fishes differs from that of their sympatric native counterparts. Assessing the extent of niche overlap between sympatric native and non-native fish serves as a valuable metric for evaluating the intensity of competition (Tran et al. 2015; Haubrock et al. 2021). In this respect, stable isotope analysis emerges as a powerful analytical tool for elucidating such interactions across various trophic levels (McCue et al. 2020; Balzani and Haubrock 2022).

The Lower Pearl River Basin of China faces a heightened risk of non-native fish invasions due to intensive aquaculture and the ornamental fish trade (Wei et al. 2019). A recent investigation revealed that 14 non-native fish species have established self-sustaining populations in the area (Wei et al. 2019). Amongst these species, Mrigal carp *Cirrhinus mrigala*, redbelly tilapia *Coptodon zillii*, Nile tilapia *Oreochromis niloticus* and armoured catfish *Pterygoplichthys* spp., which are omnivores and detritivores, have established large self-sustaining populations and co-occurred in the Pearl River Basin (Gu et al. 2020). These sympatric species have similar diets, primarily constituting of detritus, dead organisms, macroinvertebrates and aquatic plants and, accordingly, compete for food (Froese and Pauly 2023). At the same time, competitive biotic resistance, which is driven by competition amongst species exploiting the same resources, tends to be weaker in freshwater communities compared to marine and terrestrial communities due to lower species diversity and availability of unexploited niches (Moyle and Light 1996; Shurin et al. 2006; Alofs and Jackson 2014). These characteristics can accelerate the invasion of non-native species in freshwater communities (Moyle and Light 1996). On the other hand, native fish in freshwater ecosystems can be susceptible to competition with non-native fish due to the latter's advantage in terms of life-history traits (Bohn et al. 2008; Rehage et al. 2020). Studies have suggested that non-native fish are characterised by omnivory, faster growth, higher fecundity, earlier maturity, higher ability to colonise various habitats, higher tolerance to stress and higher phenotypic plasticity relative to native fish (Cucherousset et al. 2009; Liu et al. 2017). Overall, the ecological dynamics of competitive native and multiple non-native species are inherently complex, involving the interaction between native and non-native fish, as well as amongst non-native fish, making the consequences of invasions by multiple fish difficult to predict.

This study employed nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) stable isotope analysis to achieve three objectives: (i) elucidate differences in trophic characteristics between native and non-native fish at the community level; (ii) quantify the degree of

niche overlap between native and non-native fish at the community and functional feeding group levels; and (iii) determine whether native and non-native fish have similar diet composition. The outcomes of this study are expected to provide a deeper understanding of the interactions between multiple native and non-native fish, which is crucial for identifying the consequences of multiple species invasions.

Methodology

Sampling and processing

Sampling in the Lower Pearl River Basin included the rivers Beijiang, Dongjiang, Liuxihe, Xijiang, Xizhijiang and Zengjiang (Fig. 1). The region is characterised by a subtropical monsoon climate, with an annual mean temperature of 21.8 °C and mean annual rainfall of 1790 mm, primarily occurring between April and September (Li et al. 2013). In total, 551 organisms from 44 native fish species, 11 non-native fish species and 35 macroinvertebrate species of which one was non-native (Suppl. material 1: table S1) were collected together with 162 samples of basal resources from the six rivers during summer and early autumn in 2020. Only adult fish were sampled to reduce the effects of ontogeny. For the organisms, one to three individuals were sampled per species per site; for the basal resources, three samples were collected per site. Sampling at such spatial extent ensured the ability to generalise the findings from this study (e.g. Farly et al. (2019); Reis et al. (2020); Filazzola and Cahill (2021)). Fish were captured using six gillnets (mesh size 45 mm, length 5 m) and six shrimp traps (mesh size 4 mm, length 5 m), which were randomly placed at the sampling sites for ≈ 12 h. The sampled fish were moved to a portable refrigerator (–20 °C) and shipped to the laboratory. Fish were identified to species level and categorised into their predominant functional feeding group (FFG) (after Wang et al. (2019): Suppl. material 1: table S1). Standard length (SL) and body weight were measured for each specimen. A sample of dorsal muscle tissue was collected from each fish for further laboratory processing. The use of animals in this study complied with the National Research Council's Guide for the Care and Use of Laboratory Animals.

To predict the diet composition of native and non-native fish, potential food sources were collected from the six rivers where fish were sampled. Aquatic insects were captured using a D-shaped net (edge length of 30 cm and pore size of 500 μm: Rosati et al. (2016)). Snails and bivalves were sampled by hand and their soft tissues collected for isotope analysis. All macroinvertebrate specimens were identified to the lowest practical taxonomic level, typically the species and their body length and weight were measured. Macroinvertebrate taxa were categorised, based on their predominant FFG (after Tachet et al. (2002): Suppl. material 1: table S1). Riparian plants accessible to fish were also collected and identified to the species level. Plant species were classified as C3 and C4, based on their $\delta^{13}C$ value (i.e. C3 plants: –36‰ to –20‰; C4 plants: –15‰ to –7‰: Farquhar et al. (1989)). For fine particulate organic matter (FPOM), the surface layer of the sediment was agitated to suspend particles in the water and a sample of the suspension was collected in an acid-washed plastic bottle. Coarse particulate organic matter (CPOM) was manually collected. Periphyton was removed from five to six rocks using a toothbrush and the suspension was preserved in an acid-washed plastic bottle. Seston, primarily consisting of phytoplankton and detritus, was collected using a seston sampler (mesh size: 0.064 mm) and the slurry transferred to a plastic bottle that had been washed with acid. All samples were promptly preserved at –20 °C.

Figure 1. Map of the six rivers of the Lower Pearl River Basin of China sampled for native and non-native fish, macroinvertebrates and basal resources.

Stable isotope analysis

All samples were dried at 60 °C for 48 h and then ground to powder using a mortar and pestle. For small-bodied macroinvertebrates, two to three individuals were homogenised into one sample. Basal resources including CPOM, FPOM, periphyton, plants and seston were also dried, ground and acidified to remove inorganic carbon. The powdered samples were loaded into individual tin capsules and weighed. Up to three replicates of each animal species and basal resources per river were combusted. The N and C content and isotope ratios were determined using a continuous-flow carrier-gas system (Conflo) equipped with a stable isotope mass spectrometer (Delta V Advantage, Thermo Finnigan, Germany) and an elemental analyser (Thermo Fisher, USA) at Wuhan Botanical Garden, Chinese Academy of Sciences. Replicates of isotopic standard samples (urea) were processed to calibrate for any potential drift (Jackson et al. 2020). The $\delta^{15}N_{AIR}$ and $\delta^{13}C_{V\text{-}PDB}$ of urea were –0.30‰ and –42.63‰, respectively, with an uncertainty value of 0.2‰ (95% confidence level). Precisions, calculated as (SD/mean) *100, for the repeated measurements of urea, were 0.8% (n = 23) for $\delta^{15}N$ and 0.3% (n = 23) for $\delta^{13}C$.

The $\delta^{15}N$ and $\delta^{13}C$ were corrected to compare differences amongst rivers. Accordingly, $\delta^{15}N$ was converted to trophic position (TP) as per Olsson et al. (2009):

$$TP = 2 + (\delta^{15}N_{fish} - \delta^{15}N_{prey}) / 3.4,$$

where $\delta^{15}N_{fish}$ is the nitrogen stable isotope ratio of each individual fish and $\delta^{15}N_{prey}$ is the average $\delta^{15}N$ value of the macroinvertebrate prey resources from each river. In this study, the bivalves of the primary consumers and *Angulyagra polyzonata* were used in the calculation. Bivalves and *A. polyzonata*, which were widely distributed across the six rivers, are long-lived filter-feeders and have relatively simple diet sources. Note that the macroinvertebrates were enriched in $\delta^{15}N$ due

to the pollutions from domestic sewage in the Lower Pearl River (e.g. Bode et al. (2014); Xue et al. (2023)). The constant 2 is the empirical value of the trophic position of the primary consumers and the constant 3.4 is the fractionation factor between adjacent trophic levels (Post 2002). The $\delta^{13}C$ was corrected as follows:

$$\delta^{13}C_{corr} = (\delta^{13}C_{fish} - \delta^{13}C_{meanMI}) / CR_{MI,}$$

where $\delta^{13}C_{corr}$ is the corrected $\delta^{13}C$, $\delta^{13}C_{fish}$ is the $\delta^{13}C$ of each individual fish from each river, $\delta^{13}C_{meanMI}$ is the average $\delta^{13}C$ of the bivalves and *A. polyzonata* from each river and CR_{MI} is the $\delta^{13}C$ range ($\delta^{13}C_{max-}\delta^{13}C_{min}$) of the bivalves and *A. polyzonata* (Olsson et al. 2009).

Statistical analysis

Trophic characteristics

The effect of fish origin (Origin: native, non-native) and FFG on $\delta^{13}C_{corr}$ and TP was analysed by linear mixed modelling using the R package lme4. In the models, $\delta^{13}C_{corr}$ and TP were the response variables, Origin and FFG the fixed effects, River and SL the random effects, as follows:

$$\delta^{13}C_{corr} \sim Origin + FFG + Origin:FFG + 1 / River + 1/ SL$$

$$TP \sim Origin + FFG + Origin:FFG + 1 / River + 1/ SL$$

Layman metrics were computed for the native and non-native fish in each river using the R package SIBER (Layman et al. 2007). Trophic structure was described by six community-wide Layman metrics for the $\delta^{15}N$ and $\delta^{13}C$ ranges, total area (TA), mean distance to centroid (CD), standard deviation of nearest neighbour distance (SDNND) and mean nearest neighbour distance (MNND). The influence of fish origin on the Layman metrics was tested by permutational (univariate) analysis of variance, based on a one-way design using the adonis function of the vegan R package. A Euclidean distance matrix was used, with 1000 permutations of the raw data and statistical effects evaluated at $\alpha = 0.05$.

Niche overlap

The probability of overlap between the isospace of native and non-native fish was estimated by Bayesian analysis using the R package nicheROVER, which is not sensitive to sample size, with a normal-independent-inverse-Wishart prior to simulate the posterior distribution of the models' parameters (Swanson et al. 2015). The overlap metric is directional and represents the probability that an individual from Group A will be found in the niche of an individual from Group B. Niche area is defined as the region in the $\delta^{15}N$ and $\delta^{13}C$ bivariate space with 95% probability, using a Bayesian approach to account for uncertainty (Swanson et al. 2015). Mean overlap of native and non-native fish was calculated using Bayesian 95% credible intervals based on 10,000 iterations (Swanson et al. 2015). Fish niche overlap was estimated at community level and FFG level using this model. At the community level, native and non-native fish were pooled respectively for each river. The analysis was also conducted at FFG level

to investigate the interaction amongst non-native FFGs, as well as between native and non-native FFGs. Each FFG was then separated for native and non-native groups for each river. Samples with more than five individuals were included in the models. The analysis was conducted separately for each river to account for spatial variation in isotopic baselines. The probability of niche overlap between two groups was considered to be biologically significant when > 50%. Raw isotopic data were used in the analysis. In this study, a Bayesian approach was preferred over a classical (frequentist) approach owing to the small sample sizes resulting from the sampling design that accounted for the diversity of watercourses in the Lower Pearl River Basin and the community-wide extent of the analyses. The use of credible intervals (analogous to confidence intervals in frequentist statistics) was, therefore, deemed a more informative option than setting significance levels (Hilborn and Mangel 1997).

Diet composition

The relative proportions of potential sources contributing to the diet of native and non-native fish in each river were analysed using a Bayesian mixing model with R package MixSIAR (Stock et al. 2018). Estimates were based on the mean ± SD δ^{15}N and δ^{13}C of the basal resources and with Species as the random factor. Only fish species with more than three samples were selected for analysis. To account for spatial variation in the isotopic ratios of diets, food resources and fish were analysed separately for each river. Resources were pooled into six groups (i.e. C3 plants, C4 plants, CPOM/FPOM, macroinvertebrates, periphyton, seston) for each site, based on the overlap in isotopic space for the individual sources and the category of the resources (Suppl. material 1: fig. S1). All mixed models were conducted using lipid-corrected δ^{13}C values, which were adjusted, based on equations provided for macroinvertebrates (Post et al. 2007) and fish (Kiljunen et al. 2006). These adjustments were made for those cases where the C/N ratios were ≥ 3.5. Trophic discrimination factors (TDFs) of 2.38 ± 0.37‰ for δ^{15}N and 0.96 ± 0.26 ‰ for δ^{13}C were used to adjust for variation in isotopic discrimination between fish and their food sources (Wang et al. 2021). Simulation of Bayesian mixing polygons was performed for all consumers by Markov Chain Monte Carlo with 1,500 iterations to ensure all individuals fell within a 95% mixing polygon (Smith et al. 2013). The model used the Process * Residual error term for the consumer, with Process for the variation of consumer and Residual for the variation of sampling process and consumer specialisation (Stock and Semmens 2016). Uninformative priors (all values equally between 0 and 1) were used for the models. These were run using a Markov Chain Monte Carlo simulation with 50,000 to 300,000 iterations until model convergence was reached, as assessed by Gelman-Rubin and Geweke diagnostic tests (Stock and Semmens 2016). The precision of the estimates was evaluated by examining the spread of the posterior distribution (Stock and Semmens 2016).

Permutational multivariate analysis of variance was conducted with medium values using the adonis function from the vegan R package to investigate the impacts of River, FFG, Origin and their interaction terms on the potential diet contribution to the fish. A Bray-Curtis dissimilarity measure was employed, with 9999 unrestricted permutations of the raw data and with statistical effects evaluated at α = 0.05. Differences in diet composition amongst fish species were determined by their 95% credible intervals, with overlapping credible intervals indicating no differences amongst fish species (Stock et al. 2018). All analyses in this study were performed using the R language (R x64 4.1.2).

Results

Trophic characteristics

The TP and $\delta^{13}C_{corr}$ of native fish were higher, though not statistically different, than that of non-native fish (Fig. 2A, B). The TPs of invertivores and piscivores were higher than those of the other FFGs (Table 1, Fig. 2C). The TP of native piscivores was higher than that of non-native piscivores (Suppl. material 1: fig. S2). The $\delta^{13}C_{corr}$ of herbivores and omnivores were higher than that of the other FFGs (Table 1, Fig. 2D).

Layman metrics did not differ between native and non-native fish for the $\delta^{15}N$ and $\delta^{13}C$ ranges, nor for TA and CD (respectively: $F = 2.25$, $p = 0.33$; $F = 3.53$, $p = 0.17$; $F = 55.57$, $p = 0.18$; $F = 0.39$, $p = 0.58$). However, the $\delta^{15}N$ and $\delta^{13}C$ ranges of native fish were wider than those of non-native fish (Fig. 3A–D). Conversely, SDNND and MNND differed (respectively: $F = -0.73$, $p = 0.04$; $F = -0.53$, $p = 0.005$), with the native fish having lower values than non-native fish (Fig. 3E, F).

Niche overlap

At the community level, the probability that a non-native fish would be found in the niche of a native fish was higher compared to the opposite (Fig. 4, Suppl. material 1: fig. S3). River-wise, this probability was highest in Beijiang (94.6%), followed by Xizhijiang (91.2%), Dongjiang (91.1%), Zengjiang (89.2%), Liuxihe (86.3%) and Xijiang (76.97%). The probability that native fish would be found in the niche of a non-native fish was highest in Xijiang (90.4%), followed by Xizhijiang (83.0%), Liuxihe (81.0%), Beijiang (78.1%), Zengjiang (75.9%) and Dongjiang (43.8%).

At the FFG level, the niche space of non-native detritivores and omnivores significantly overlapped with that of the other native FFGs (Fig. 5A, B). In Beijiang, non-native detritivores occupied 78.93% of the niche space of native planktivores, 90.85% of native piscivores, 92.86% of native invertivores and 97.46% of native omnivores. Non-native omnivores occupied 71.48% of the niche space of native piscivores, 72.92% of native planktivores, 74.30% of native invertivores and 88.27% of native omnivores. On the other hand, native omnivores, invertivores and piscivores occupied 64.80%, 73.75% and 81.93% of the niche space of non-native detritivores, respectively. Native piscivores occupied 58.24% of the niche space of non-native omnivores. Non-native omnivores occupied 59.60% of the niche space of non-native detritivores, while non-native detritivores occupied 55.64% of the niche space with non-native omnivores. The niche sizes of these non-native fish were similar, except for the niche size of native planktivores which was smaller than that of native omnivores (Fig. 5C, Suppl. material 1: table S2).

In Dongjiang, non-native detritivores occupied 67.73% of the niche space of native omnivores, while native detritivores and planktivores occupied 51.00% and 72.76% of non-native detritivores. The niche sizes of these non-native fish were similar, except for the niche size of native detritivores which was smaller than that of native omnivores (Fig. 5D, Suppl. material 1: table S2). In Liuxihe, non-native detritivores occupied 62.74% of the niche space of planktivores and 72.57% of native omnivores. On the other hand, native planktivores, omnivores, invertivores and piscivores occupied 76.88%, 77.98%, 83.58% and 91.79% of the niche space of non-native detritivores, respectively. The niche sizes of these non-native fish were similar, except for the niche size of native invertivores which was smaller than that of non-native detritivores (Fig. 5E, Suppl. material 1: table S2).
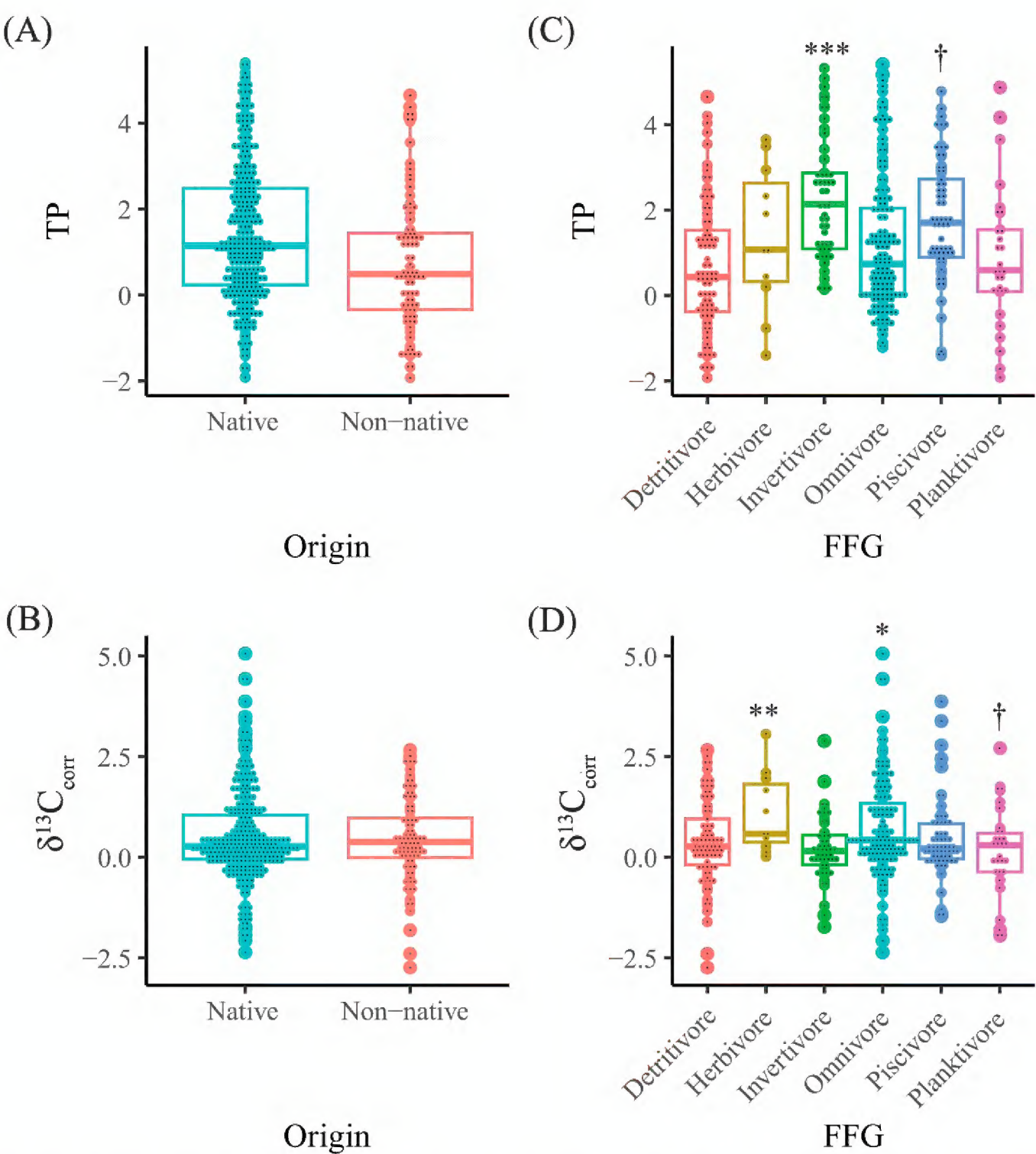
Figure 2. Differences between native and non-native fish in trophic position (TP) and corrected $\delta^{13}C$ and amongst functional feeding groups (FFG). Significant effects are indicated as *** $p < 0.001$, ** $p < 0.01$ and † $p < 0.1$.

Table 1. Fixed and random effect coefficients for a linear mixed model describing the effect of Origin (native, non-native), functional feeding group (FFG) and their interaction on trophic position (TP) and corrected $\delta^{13}C$ ($\delta^{13}C_{corr}$) for fish in six rivers of the Lower Pearl River Basin of China. SL = standard length. See also Fig. S2. Significant results indicated as *** ($p < 0.001$), ** ($p < 0.01$), * ($p < 0.05$) and † ($p < 0.1$).

Effect	Source	TP	$\delta^{13}C_{corr}$
Random	SL	0.11	0.03
	River	0.79	0.82
Fixed	Intercept	1.64	0.76
	Origin (Native)	0.61	0.56
	FFG (Herbivore)	-0.33	3.24**
	FFG (Invertivore)	3.41***	-0.36
	FFG (Omnivore)	1.52	2.10*
	FFG (Piscivore)	-1.67†	1.10
	FFG (Planktivore)	0.03	-1.84†
	Origin (Native) * FFG (Omnivore)	-0.87	-0.22
	Origin (Native) * FFG (Piscivore)	2.34*	-0.43

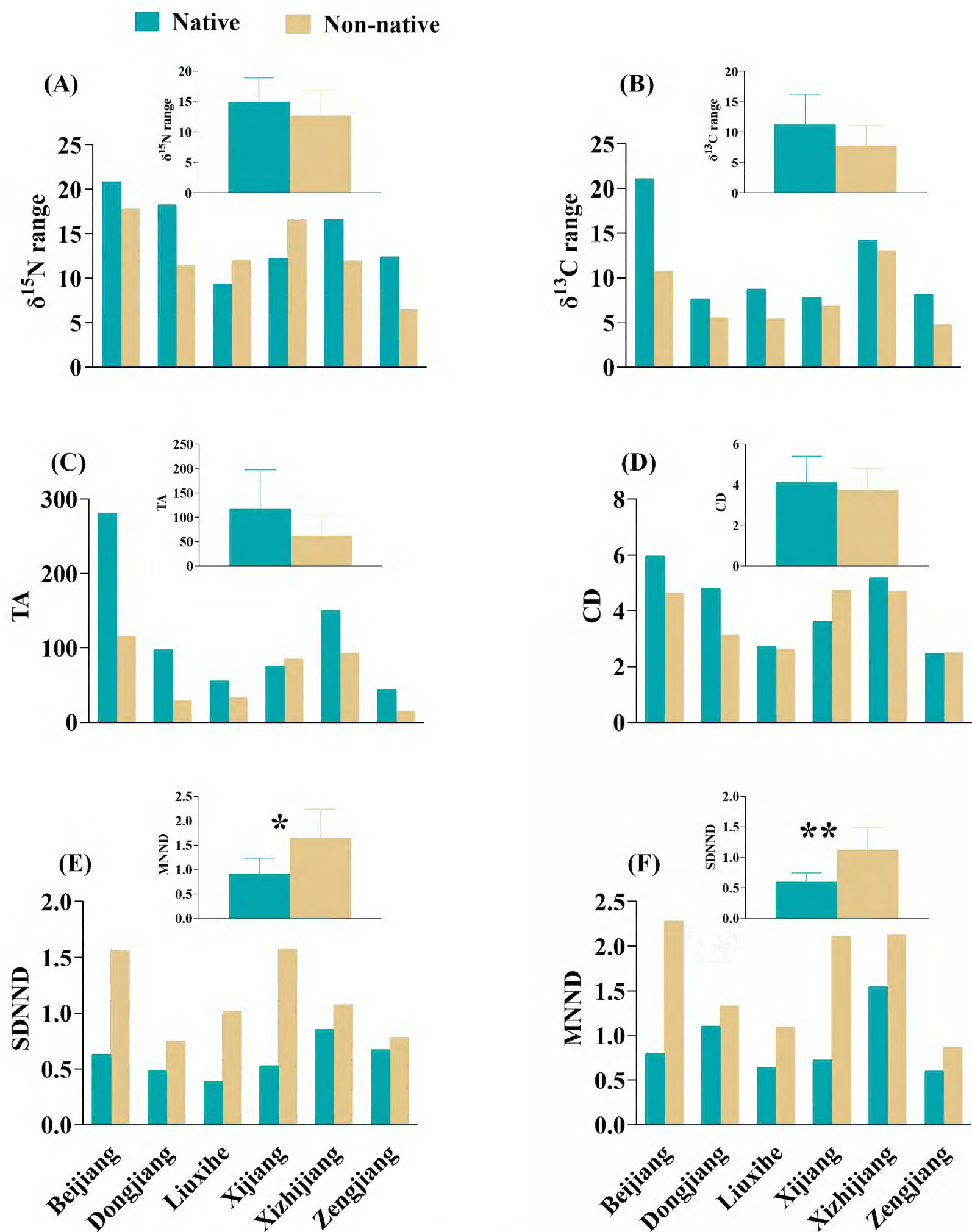**Figure 3.** Layman metrics for native and non-native fish for: (A) δ^{15}N range, (B) δ^{13}C range, (C) total area (TA), (D) mean distance to centroid (CD), (E) standard deviation of nearest neighbour distance (SDNND), (F) mean nearest neighbour distance (MNND). Insets show the Layman metrics pooled across the six rivers. Significant effects at $p \leq 0.05$ are marked with an asterisk, at $p \leq 0.01$ marked with two asterisks.

In Xijiang, non-native detritivores occupied 72.57% of the niche space of native omnivores. On the other hand, native planktivores, piscivores and omnivores occupied 75.30% 85.98% and 88.94% of the niche space of non-native detritivores, respectively, while native planktivores, omnivores and piscivores occupied 59.74%, 69.94% and 82.82% of non-native omnivores, respectively. Non-native detritivores occupied 74.35% of the niche space of non-native omnivores, while non-native omnivores occupied 66.31% of non-native detritivores. The niche sizes of these non-native fish were similar, except for the niche size of native planktivores which
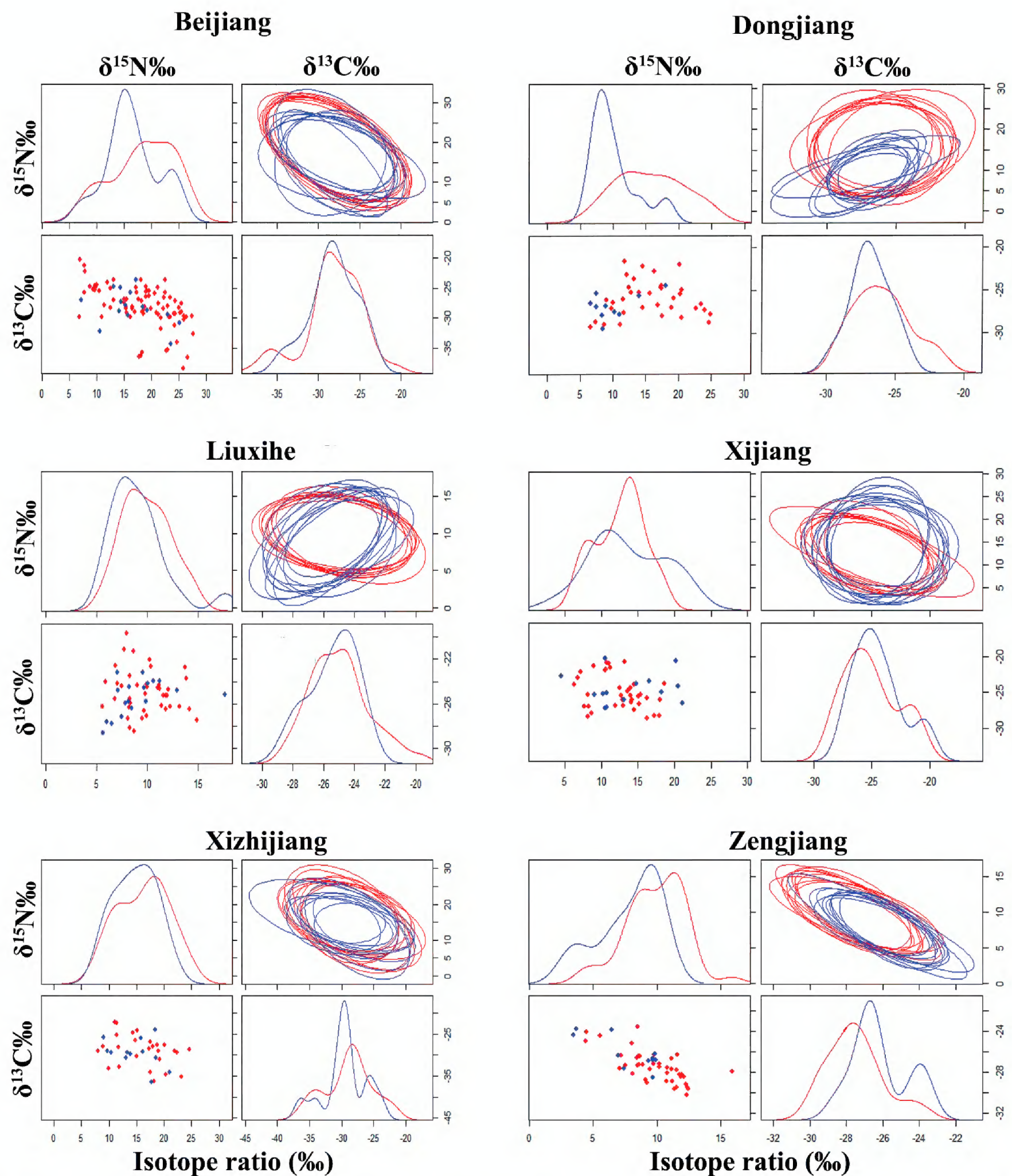
Figure 4. Bi-dimensional projections (with 95% CI) of the $\delta^{15}N$ and $\delta^{13}C$ isotopic niche region for native (red) and non-native (blue) fish.

was smaller than that of non-native detritivores and native omnivores (Fig. 5F, Suppl. material 1: table S2). In Xizhijiang, non-native detritivores occupied 88.15% of niche space of native omnivores, whereas native omnivores occupied 59.61% of non-native detritivores. The niche size of native omnivores was similar with that of non-native detritivores (Fig. 5G, Suppl. material 1: table S2). In Zengjiang, non-native detritivores occupied 98.75% of the niche space of native omnivores. On the other hand, native planktivores occupied 96.34% of the niche space of non-native detritivores. The niche sizes of these non-native fish were similar, except for the niche size of native omnivores which was broader than non-native detritivores and native invertivores (Suppl. material 1: table S2, Fig. 5H).
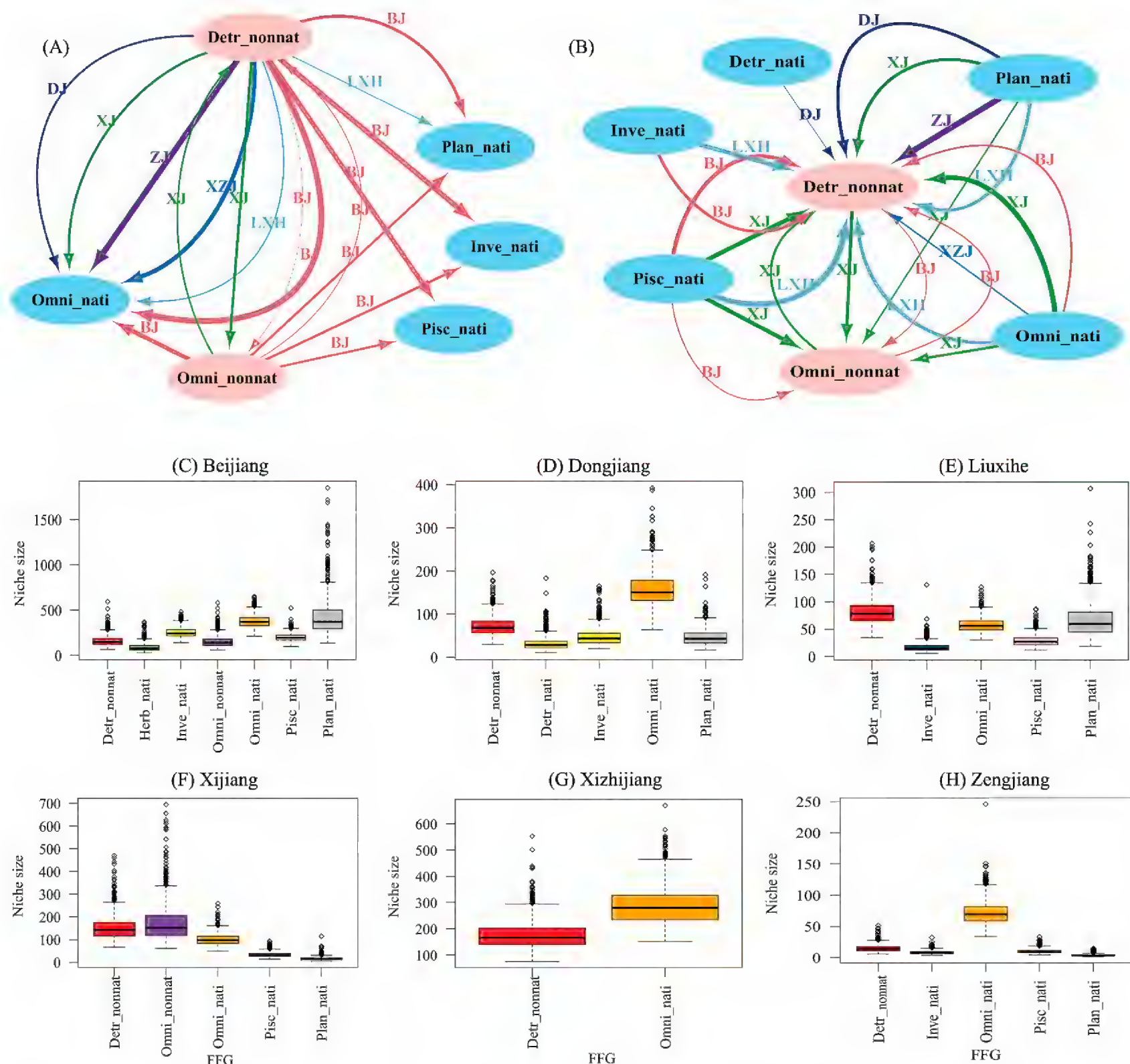
Figure 5. Niche overlap estimates and niche size of native and non-native functional feeding groups (FFG). Only estimates > 50% are shown. (A) Probability of non-native fish FFGs (light red) overlapping with native fish FFGs (light blue) indicated by the direction of the arrows. Line thickness indicates the degree of niche overlap with rivers labelled above the lines. (B) Probability of native fish FFGs overlapping with non-native fish FFGs. (C-H) Niche size of overlapping functional feeding groups in the six rivers. The differences in niche sizes among FFGs can be found in Table S2. Fish FFG abbreviations: Detr_nat = detritivorous native; Detr_nonnat = detritivorous non-native; Herb_nat = herbivorous native; Inve_nat = invertivorous native; Omni_nat = omnivorous native; Omni_nonnat = omnivorous non-native; Pisc_nat = piscivorous native; Plan_nat = planktivorous native. River abbreviations: BJ = Beijiang; DJ = Dongjiang; LXH = Liuxihe; XJ = Xijiang; XZJ = Xizhijiang; ZJ = Zengjiang.

Diet composition

River significantly affected the potential diet composition of fish, but not the interactions with Origin and FFG (Table 2). The difference in diet composition between some native and non-native fish depended on the category of diet source across the rivers (Fig. 6, Suppl. material 1: tables S3–S8). In Beijiang, the potential food sources contributed equally to the diet of native and non-native fish, except for macroinvertebrates (Fig. 6A, Suppl. material 1: table S3). *Pterygoplichthys* spp. had a higher probability to consume macroinvertebrates than native omnivores *Acheilognathus macropterus*, *Osteochilus salsburyi*, large-scale loach *Paramisgurnus dabryanus*, the non-native omnivore streaked prochiloid *Prochilodus lineatus*, the invertivore *Hemibarbus umbrifer*, as well as Hong Kong catfish *Clarias fuscus* and

Table 2. Permutational multivariate analysis of variance for the effect of River, functional feeding group (FFG), Origin (native, non-native) and their interaction terms on the diet composition (i.e. median diet proportions) of fish. Significant effects (α = 0.05) in bold.

Source	df	R^2	F	p
River	5	0.330	8.88	**< 0.01**
FFG	5	0.050	1.42	0.12
Origin	1	0.001	0.20	0.93
River*FFG	18	0.110	0.86	0.77
River*Origin	5	0.050	1.37	0.14
FFG*Origin	2	0.010	0.87	0.53
River*FFG*Origin	3	0.004	0.18	1.00
Residual	91	0.390		

Amur catfish *Silurus asotus*. In Dongjiang, the probabilities of all potential food sources contributed equally to the diet of native and non-native fish, except for macroinvertebrates (Fig. 6B, Suppl. material 1: table S4). The non-native detritivores *C. mrigala*, *O. niloticus* and *Pterygoplichthys* spp. had a lower probability to consume macroinvertebrates relative to the native omnivore *Megalobrama terminalis*. In Liuxihe, the probabilities of all potential food sources contributed equally to the diet of native and non-native fish, except for C4 plant. Native omnivore *P. dabryanus* had a higher probability to consume C4 plants than non-native detritivores *C. mrigala* and *Pterygoplichthys* spp (Fig. 6C, Suppl. material 1: table S5). In Xijiang, no difference was found in the probability of diet contribution between native and non-native fish (Fig. 6D, Suppl. material 1: table S6). In Xizhijiang, the potential diet contributed in similar probabilities to that of native and non-native fish, except for CPOM/FPOM (Fig. 6E, Suppl. material 1: table S7). The non-native detritivore *C. mrigala* had a higher probability to consume CPOM/FPOM than the native omnivores *A. macropterus* and *Carassioides acuminatus*, the planktivore silver carp *Hypophthalmichthys molitrix*, the invertivore zig-zag eel *Mastacembelus armatus* and the non-native omnivore *C. zillii* and detritivore *Pterygoplichthys* spp. Native detritivore *Cirrhinus molitorella* had a higher probability to consume CPOM/FPOM than non-native *C. zillii* and *Pterygoplichthys* spp. In Zengjiang, the potential food source contributed in similar probabilities to the diet between native and non-native fish, with the exception of C3 plants and CPOM/FPOM (Fig. 6F, Suppl. material 1: table S8). The non-native piscivore African sharptooth catfish *Clarias gariepinus* had less probability to consume C3 than the native piscivores *Hemibagrus macropterus*, yellow catfish *Tachysurus fulvidraco*, the invertivores *Eleotris oxycephala*, *M. armatus* and *Rhinogobius giurinus*, while it had a higher probability to consume CPOM/FPOM than these piscivores and invertivores.

Discussion

Although previous studies have indicated that the invasion of non-native fish may lead to a reduction in the trophic position of native fish species as a result of interspecific competition (Britton et al. 2018), the current study observed that, despite no significant differences, these non-native fish tended to occupy a lower trophic position relative to the native fish. In the Lower Pearl River Basin, non-native fish species, associated with aquaculture and aquarium trade, are primarily detritivores
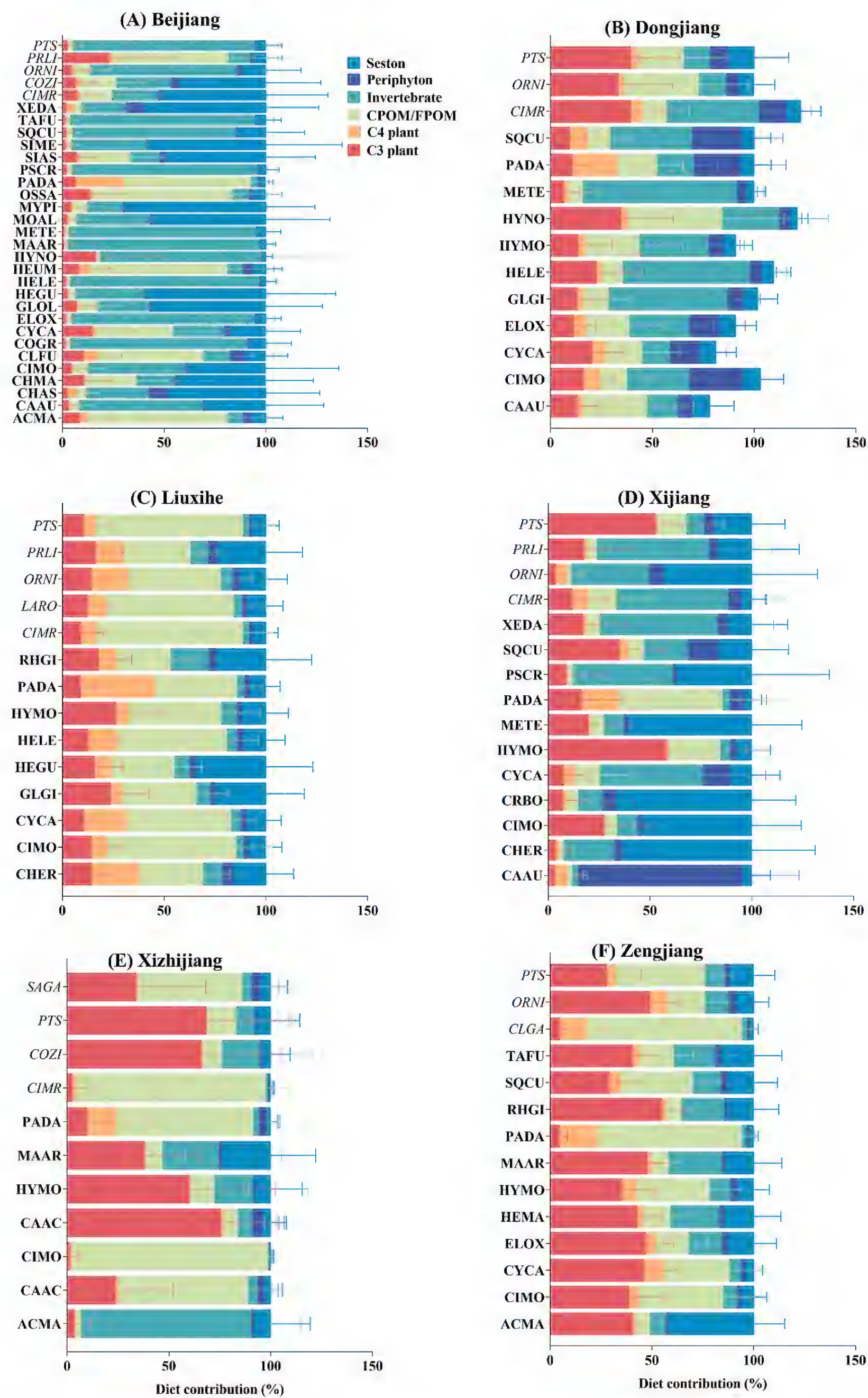
Figure 6. Comparison of the probability of diet contribution between native (bold) aquatic organisms and non-native (italics) fish. Species name abbreviations in Suppl. material 1: table S1.

and omnivores, contrasting with other study areas where non-native fish are predominantly piscivorous and associated with recreational fishing activities (Eby et al. 2006; Cucherousset et al. 2012). The occupancy of lower trophic positions by non-native fish may confer an advantage, as they can exploit more readily available basal resources such as detritus, plants and algae within the recipient ecosystem (Moyle and Light 1996; Gido and Franssen 2007; Liew et al. 2016). These basal resources typically exhibit lower $\delta^{15}N$ than animal prey, which consequently leads to fish that consume these resources having lower $\delta^{15}N$, thereby occupying a lower trophic position (Post 2002). In this regard, non-native piscivore (i.e. *C. gariepinus*) occupied a significantly lower trophic position than native piscivores, which is consistent with its diet preference on $\delta^{15}N$ depletion diets in the invaded rivers (e.g. Low et al. 2022). Utilisation of basal resources could have contributed to the observed trophic overlap in this study between native and non-native fish, as these resources are also essential for the native fish.

No discernible differences in trophic structure and diet composition were observed between native and non-native fish, leading to a high degree of overlap. These findings suggest that both native and non-native fish may face intense competition. Although some native fish exhibited distinct dietary composition from non-native fish across the study rivers, native fish species may confront heightened competition not only from non-native fish, but also amongst themselves. This is attributable to the increased trophic redundancy within the native fish community, with native fish depending on a limited subset of resources (Layman et al. 2012). Thus, native fish are anticipated to experience exacerbated adverse effects from interspecific competition.

Interspecific interactions between native and non-native fish have been shown to result mainly in negative or neutral impacts (Bohn et al. 2008; Jackson et al. 2016). The exclusion of native fish due to competition with non-native fish may not be immediately apparent when food resources are readily available to both native and non-native fish (Britton et al. 2019). In this study, at the community level, non-native fish had a higher probability to occupy the niche space of native fish than the opposite scenario. This result suggests that the ecological niche space of native fish may be reduced. Studies have demonstrated that fish invasions have resulted in dietary changes and trophic niche reduction of native fish (e.g. Parvez et al. (2023); Quintana et al. (2023)). Nonetheless, not all non-native FFGs had a high likelihood of encroaching upon the niche space of native FFGs in this study. This observation suggests that extrapolating community-level interaction outcomes from interactions at the FFG level can result in estimation errors. This is because the stable isotope spaces of communities are made of points clustered by species. Additionally, the species in two communities could be separated by empty space. Thus, the stable isotope spaces of two communities may overlap without any actual species overlap. Consequently, studies should focus on community-level interactions to gauge more accurately the collective impacts of multiple fish invasions.

The use of FFG level analysis clarifies interactions between native and non-native fish in the Lower Pearl River Basin. Non-native detritivorous fish had a high probability to occupy the niche space of native FFGs. The non-native detritivorous fish *C. mrigala*, *O. niloticus* and *Pterygoplichthys* spp. are the most abundant non-native fish species in the Pearl River Basin (Gu et al. 2019). Despite detritus representing the primary component of their diet, these species demonstrate a high degree of dietary plasticity, which allows them to incorporate a diverse array of food sources into their diet. For example, as a detritivorous fish, *Pterygoplichthys* spp.

were anticipated to feed primarily on detritus and algae (Froese and Pauly 2023). However, based on gut content analysis, *Pterygoplichthys* spp. have been found to consume also benthos, plants and carcasses (Reinas et al. 2022). The results of stable isotope analysis in this study revealed that macroinvertebrates made a relatively high contribution to the diet of *Pterygoplichthys* spp. in Beijiang, where richness and abundance of macroinvertebrates are high. While *O. niloticus* may not directly impact piscivorous fishes and major carps, its trophic niche has been found to overlap with that of native fishes due to its adaptable feeding habits (Khan and Panikkar 2009; Henson et al. 2018). *Cirrhinus mrigala* also exhibits a broad dietary spectrum, with its primary food sources encompassing a variety of plant matter, invertebrates, algae and zooplankton (Zhang et al. 2024). All of this could explain why non-native detritivorous fish can colonise the trophic niche of a diverse array of native fish in different FFGs.

The niche space of native omnivorous fish was relatively broader than that of non-native detritivorous fish in Zengjiang, which might mitigate the competitive pressure exerted by non-native fish. Native omnivorous, piscivorous and planktivorous fish also had high probabilities of occupying the niche space of non-native detritivorous and omnivorous fish. These results suggest that non-native fish might also face intense competition from native fish. Overall, this study has revealed that non-native fish have established novel trophic interactions with native fish within the community. However, observations also indicated that some native FFGs demonstrated minimal interactions with non-native FFGs, suggesting variability in the degree of ecological integration (see Suppl. material 1: fig. S3). This variability depends on factors such as quantity and quality of food resources within the habitat, degree of environmental disturbance as well as foraging strategies and population density (Liew et al. 2016; Wang et al. 2019; Almela et al. 2021; De Santis et al. 2021). Fish species, especially those occupying specialised trophic niches, may be more vulnerable to the adverse effects of interactions with non-native fish (Almela et al. 2021). Conversely, species with a wider dietary breadth generally exhibit greater resilience against competitive pressures by non-native species (Collier et al. 2018). However, native fish species whose trophic niche sizes are similar to those of non-native fish may face direct competition in their diet (Harris et al. 2022). These findings suggest that novel interactions between native and non-native fish can lead to a dynamic equilibrium within the community rather than causing its collapse (e.g. Alofs and Jackson (2014)).

Co-occurring non-native fish species have the potential to alter community structure through direct or indirect interactions, either facilitating or suppressing one or both invaders (Coughlan et al. 2022; Crone et al. 2023). A meta-analysis has shown that the majority of interactions amongst invaders are neutral (Jackson 2015). This study has revealed a significant trophic niche overlap, exceeding 50%, between non-native detritivorous and omnivorous fish. This finding suggests the potential for competition amongst these non-native fish, as they have similar dietary and niche size.

Conclusions

Understanding the consequence of interactions between multiple non-native fish and native aquatic organisms is a major challenge to manage multiple invasions (e.g. Guareschi et al. (2021)). The results of this study have suggested

that native and non-native fish may experience intense competition from each other due to their similar trophic characteristics. Some native fish might alleviate the impacts from non-native fish due to their larger niche size. Some native and non-native fish have different types of foraging behaviour and can use distinct food resources to avoid direct competition (e.g. Zaia Alves et al. (2020)). In this study, the trophic niche of non-native detritivorous fish was significantly overlapped with distinct FFGs, such as invertivores, piscivores and planktivores, which have different trophic traits and foraging behaviour (Froese and Pauly 2023). The interspecific competition amongst non-native fish might also alleviate the negative impacts of non-native fish on native fish (e.g. Van Zwol et al. (2012); Liu et al. (2018)). Albeit limited, the present findings suggest that trophic interaction between native and non-native fish is likely to reach a dynamic equilibrium status in the community owing to the trophic segregation of fish species and antagonistic effect amongst non-native fish.

Acknowledgements

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Funding

Author contributions

H. Wei and D. Gu-Conceptualization; Investigation; Data curation; Methodology; Writing-original draft; Funding acquisition. L. Villizi- Data curation; Writing- review & editing. M. Zhang, Y. Jiang, M. Xu, M. Fang, F. Yu, L. Su and X. Wang- Investigation, Writing- review & editing.

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Data availability

The datasets and R code generated in this study are available from the first author upon request.

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Supplementary material 1

Additional information

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Data type: docx

Explanation note: This file includes three supplementary figures and eight tables. The titles of the figures and tables are listed as following: **fig. S1.** Biplot of δ^{15}N vs δ^{13}C for food resources. **fig. S2.** Differences in trophic position (left) and corrected δ^{13}C‰ (right) between native and non-native detritivore, omnivore and piscivore fish. **fig. S3.** Niche overlap estimates of native and non-native functional feeding groups in six rivers of the Lower Pearl River Basin of China. **table S1.** Fish and macroinvertebrates, with indication of feeding group and origin, sampled from the Lower Pearl River Basin of China. **table S2.** The mean, standard error and 95% credible intervals of the niche size for native and non-native functional feeding group in six rivers. **tables S3–S8.** MixSIAR results for the probability of diet contribution for native and non-native fish in Beijiang, Dongjiang, Liuxihe, Xijiang, Xizhijiang and Zengjiang. Species name abbreviations in table S1.

Link: https://doi.org/10.3897/neobiota.96.129121.suppl1